MORPHOLOGICAL AND ANATOMICAL STUDIES OF THE VEGETATIVE ORGANS OF RHEXIA

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(WITH PLATES I AND II)

An anatomical classification of the Melastomaceae has been proposed by VAN TIEGHEM,[1] who divides the family into two tribes: Melastomeae and Memecyleae. In the former the secondary hadrome shows the normal structure, while in the latter the secondary hadrome incloses groups of leptome in as many concentric bands as the stem shows annual rings. The Melastomeae comprise four subtribes: Dermomyelodesmeae, with supernumerary mestome strands in the cortex and pith; Dermodesmeae, with supernumerary mestome strands in the cortex alone; Myelodesmeae, with supernumerary mestome strands in the pith alone; and Adesmeae, without supernumerary mestome strands. The Memecyleae comprise two subtribes: Pternandreae, without sclereids in the leaves; and Mouririeae, with sclereids in the leaves. The genus Rhexia belongs to the Dermomyelodesmeae.

Among other anatomical works may be mentioned those by PFLAUM,[2] PALÉZIEUX,[3] and VÖCHTING,[4] and also a very detailed diagnosis of the family in SOLEREDER'S *Systematische Anatomie der Dicotyledonen* (p. 405).

It would thus appear as if the family had already been treated to such an extent that little if anything of real importance could be added, a fact fully appreciated by the author. However, the study of internal structure is not always accompanied by a corresponding treatment of the external, and so far the Melastomaceae have not

[1] Classification anatomique des Melastomacées. Bull. Soc. Bot. France **38**: 114. 1891.

[2] Anatom.-systemat. Untersuch. d. Blattes der Melastomaceen. Diss. München, 1897.

[3] Anatom.-systemat. Untersuch. d. Blattes der Melastomaceen. Bull. Herb. Boiss. 7: appendix v. 1899.

[4] Der Bau und die Entwickelung des Stammes der Melastomaceen. Hanstein's Bot. Abhdl. **3**:1. 1878.

yet been thoroughly investigated. The monograph contributed by COGNIAUX[5] is purely systematic and adds nothing to the natural history of these interesting plants. Copious as is the literature, very little attention has been paid to the following questions: how the plants grow, how they develop from seeds to mature plants, and how well the structural characteristics are preserved under various conditions.

Although the family is most widely distributed in America, very few species occur north of the tropics, and Rhexia is the only genus that occurs in the United States and Canada, with about ten species. Two of these, *R. virginica* and *R. mariana*, occur in the District of Columbia, the former extending as far north as Ontario, the latter to New Jersey. They both inhabit sandy swamps, associated with *Lilium superbum*, certain Cyperaceae (Scleria, Fimbristylis, Scirpus, and Carex), Polygalaceae, Violaceae, etc.

Having had the opportunity of studying these two species in the field at various seasons, I have found several points in their external structure which have not hitherto been described, and which may serve as a small contribution to the knowledge of the life-history of these interesting plants. To this is added a brief anatomical description of the vegetative organs, and especially of the roots, since these have not been studied heretofore.

Rhexia virginica L.

While studying the vegetative propagation exhibited by representatives of the local flora, I never was able to find any specimen of this species with a rhizome as described in the various manuals. According to BRITTON, GRAY, and SMALL, this species should possess "horizontal, slender, and tuberiferous rootstocks." That this statement is very incorrect may be seen from the following notes, in which I shall endeavor to show that the underground organs described as tuberiferous rootstocks are simply tuberous roots; and that the development of root-shoots is of great importance to the plant, being its only means of vegetative propagation.

Root-shoots of adult specimens, like those of *figs. 3* and *4*, do not give any clear idea of the remarkable way in which this herbaceous

[5] DeCandolle's Monogr. phanérog. 7:385. 1891.

plant persists. In *fig. 3* a root-shoot is represented which at first glance may suggest a "slender tuberiferous rootstock" with a basal stem-portion, subterranean and covered with scale-like leaves. In *fig. 4*, however, a larger tuberous body is seen, from which several stems have developed, whose irregular position does not indicate that they have arisen from the axils of opposite leaves. As a matter of fact, there are neither leaves nor leaf scars to be observed upon this tuberous organ. The "rhizome" represented in *fig. 4* is the one most frequently found in flowering or fruiting specimens. A closer examination shows that the tuberous organs are not tubers, but tuberous roots. Moreover, in *fig. 3* the small tuberous body is borne upon a slender branch, which is seen to be a secondary root and not a stolon, since it bears no leaves. If these organs were stems, they would have been provided with opposite leaves like those of the aerial shoots, and the shoots would necessarily have occupied a much more definite position than those shown in *fig. 4*. Moreover, the internal structure of these organs proved to be that of a true root. This is the only type of "rhizome" that I have found in the very many flowering and fruiting specimens examined.

The development of root-shoots is a phenomenon very frequently observed in our herbaceous and woody plants, but thus far we know a very limited number of plants that persist only as root-shoots. It was very desirable, therefore, to study the younger stages and especially the seedlings of Rhexia. On account of their diminutive size they are difficult to find in nature, since they are always more or less hidden by the rank vegetation that covers the swamps. However, I succeeded in detecting some small patches of young plants among which there were many seedlings. One of these is shown in *fig. 1*, which represents the complete root system, the very small epigeic cotyledons (*Cot*), and the basal internodes of the aerial shoot. At this stage the primary root (R) is the main root of the young shoot; it bears several lateral and very thin branches, two of which are opposite and developed beneath the cotyledons. These two roots commence to swell, and during the summer they show a local thickening in the shape of a fusiform tuber (r). A few secondary roots sometimes develop from the first internode a short distance above the cotyledons. At the end of the first season the shoot dies down to the ground, and

the primary root withers with the exception of the two lateral swollen branches, which winter over as two separate roots.

In the following spring a young shoot develops, with scale-like, opposite leaves at the basal nodes, and with several pairs of secondary roots from the nodes, while a dark-colored tuberous body occurs at the base of the shoot. One or more of the secondary roots soon commence to increase in thickness, forming fusiform tubers like the one described above on the root of the seedling. *Fig. 2* shows a root-shoot; the short, dark tuber at the base of the shoot represents the lateral tuber of the seedling (*r* in *fig. 1*), and the shoot is developed not from the base of the tuber but from its upper face. If the shoot had continued the axis of the swollen root, there would have been a persistent primary root, but such a case was not observed; the shoot invariably occupied the position shown on the root marked *r* in *fig. 2*, where a bud is seen near the base on the upper face of the tuber. This bud is to develop a new and independent plant during the next year.

The specimen thus described (*fig. 2*) represents the root-shoot of the seedling and lives only one year, the persisting part belonging to a secondary root. Older specimens, like those in *figs. 3* and *4*, show the same course of development, but the shoots are more vigorous and the tuberous roots much larger. The secondary roots develop in pairs from the nodes, between the opposite scale-like leaves. These roots are quite long, branch freely, and are able to produce shoots as described above. Although the underground portion of the stem bears several leaves, none of these were found to subtend buds, and the shoot dies down completely at the end of the season. The tuberous roots, on the other hand, may live for three years, if not longer; the large specimen represented in *fig. 4* was fully three years old. When these root-tubers persist for more than two years they develop several shoots (*fig. 4*), and several strong, amply branching, lateral roots.

An over-wintering stage is shown in *fig. 5*. The tuber occupies here a horizontal position, and the shoots for the next year are already visible as buds on small stems with scale-like leaves and quite distinct internodes; the place of development of these minute shoots is along the upper face of the root. It is only when the tuber occupies a more or less vertical position that the shoots show a tendency to push out from near the apex, as may be seen in *fig. 3*.

Rhexia virginica, therefore, exhibits a very singular type of vegetative propagation, that is, one restricted entirely to the development of root-shoots.

THE INTERNAL STRUCTURE OF THE VEGETATIVE ORGANS

The roots

The secondary and lateral roots and the slender portions (apical and basal) of the tuberous roots have the same structure, modified only by age. In the tubers, on the other hand, there is a very different structure, since they remain active for a longer time and are the seat of a continuous development of aerial shoots, vegetative or floral. In the capillary lateral roots the primitive root structure remains unchanged, since they persist only one season. In the slender secondary and stronger lateral roots, which develop from the tuberous portion, the structure becomes changed at an early stage on account of the development of cambial strata from the conjunctive tissue on the inner face of the leptome strands, resulting in an increase in thickness of the stele and a gradual obliteration of the primitive structure. These roots may persist and remain active, therefore, for a longer time than do the capillary roots. However, the increase in thickness of the stele does not always cause a rupture of the surrounding tissues, accompanied by secondary formation (cork and secondary cortex); the endodermis, cortex, exodermis, and epidermis often remain entire for some time. As soon as the development of cork commences (in Rhexia from the pericambium), the peripheral tissue necessarily becomes broken, though without being thrown off.

A much greater increase in thickness is seen, of course, in the tuberous roots. In them, even during the very first period of their growth, the activity of the pericambium is so rapid that the peripheral tissues from endodermis to epidermis are thrown off completely, and are replaced by strata of cork and secondary cortex originating from the pericambium. Hence the structure of the tuberous roots shows a marked deviation from that of the other roots. In *fig. 10* there are shown the several layers of cork (P), the broad parenchyma of secondary cortex (C), and a continuous circle of cambium strata surrounding a broad cylinder of thin-walled parenchyma in which the long but very narrow rays of mestome radiate from the primitive root-stele.

The number of mestome strands varies in accordance with the thickness of the tuber; the largest number observed was ten, representing the growth of one season.

The minor structure of these various tissues seems to be very uniform. The absence of ducts, stereids, and sclereids makes the structure quite simple. The epidermis is sparingly hairy or perfectly smooth. The exodermis is thin-walled and consists of one layer of cells pentagonal in cross-section, whose walls are not contractile. The cortex is thin-walled throughout and frequently shows radial collapsing; some of the cells contain druids of calcium-oxalate, but no deposits of starch. The endodermis is thin-walled also and shows the Casparyan spots very plainly; it surrounds a continuous pericambium of a single layer. A few strata of more or less thick-walled conjunctive tissue occur in the center of the stele and between the leptome and hadrome. In the tuberous roots the cork is well represented (*figs. 11* and *12*), and the secondary cortex is compact, though exceedingly thin-walled (*C* in *fig. 10*). The secondary leptome (*L* in *fig. 10*) shows a very few cells, and the hadrome (*H* in *fig. 10*) consists of several wide vessels separated by thin-walled parenchymatic tissue and by very broad rays of radially stretched parenchyma between the mestome bundles.

The section shown in *fig. 10* is from the tuberous root of the young shoot shown in *fig. 2*, upon which a small bud is visible. The root is in its second year and shows the enormous increase in proportion to the very narrow primitive stele with the short rays of hadrome (*PH* and *H*). The other section (*fig. 13*) is from an older and much thicker tuberous root, in which the number of vessels is larger and the leptome much better represented (*L*).

Although parenchymatic tissues attain a high development in these tuberous roots, they were never observed to contain any deposits of starch. It is to be noted also that these tissues are peripheral, surrounding the primitive stele, and that the central portion of the stele has no pith, but only a few strata of conjunctive tissue.

The stem

All the internodes are four-winged, while the body of the stem is cylindric. The cuticle is thin, but wrinkled; the cells of the epider-

mis are small, and moderately thickened in the wings. Hairs of two kinds are frequent: short and clavate ones (*fig. 9*), and some very long ones, with slender pluricellular stalk and a small globular head, the apical cells being extended into papillae (*fig. 6*); they both represent glandular hairs. The cortex is thin-walled and contains chlorophyll, besides druids of calcium oxalate; no palisades were observed. A thin-walled endodermis surrounds the stele, which is composed of bicollateral mestome strands, with the medullary rays narrow and thick-walled. The inner leptome represents much larger groups than the outer, and an isolated leptomatic strand (*fig. 14*) occupies the center of the pith. This central leptome may be followed through the entire length of the stem, but in the basal internodes it is accompanied by a few vessels which it partly surrounds; thus the structure becomes approximately hadrocentric. The pith is thin-walled and contains neither starch nor druids.

As a member of the Dermomyelodesmeae, Rhexia possesses also some mestome strands in the cortex, and these occur in this species only in the wings, three in each wing and very small, but containing a few elements of leptome and hadrome.

With the exception of an occasional thickening of the cortex in the wings, like a very feeble collenchyma, there is no mechanical tissue; in the basal internodes the epidermis and cortex are thrown off, while the endodermis remains intact and about four layers of pericyclic cork are developed. It is in these internodes that a central mestome strand occurs, with both leptome and hadrome.

The shoot is terminated by a flower whose peduncle, although a direct continuation of the stem, shows a somewhat modified structure. It is cylindric, but wingless, and the cortex contains no chlorophyll. The mestome strands are bicollateral, but the inner leptome forms an almost continuous band close to the hadrome, while in the stem internodes the inner leptome occurs as several distinctly separate strands. No central leptomatic strand was observed in the pith.

The leaf

The structure is bifacial. The cuticle is wrinkled on the upper face, but does not show any prominent striation. Viewed *en face* the lateral cell walls of the epidermis are undulate on the dorsal

surface but straight on the ventral; the outer cell wall is moderately thickened, and the lumen of the cells is much wider on the upper than on the lower face. Hairs like those described above are frequent, but the clavate ones occur only on the dorsal face, where the stomata also occur. These are level with the epidermis and are surrounded mostly by four cells of the same structure as the other epidermal cells, that is, the lateral walls are prominently undulate. There is a typical palisade tissue of one layer, and beneath this a pneumatic tissue of about four strata with very wide intercellular spaces. Viewed *en face* the cells of the pneumatic tissue are star-shaped, interspersed with roundish cells containing druids of calcium-oxalate. A very different structure is to be observed in the median portion of the blade, where the very broad midrib is located. The cuticle is here wrinkled on both faces, and the lumen of the epidermal cells is narrow. A large colorless parenchyma forms a broad keel underneath the midrib, and is thin-walled except where it borders the epidermis. No true collenchyma, however, is developed in any part of the blade, and no stereome. The midrib has no parenchyma sheath and contains one broad, arch-shaped, bicollateral mestome strand and a small supernumerary (*fig. 15*). This small mestome strand shows the leptome above the hadrome, and is separated from the midrib by a few strands of colorless tissue.

The very prominent lateral ribs show the same structure as the median, being bicollateral and covered by a colorless tissue on both dorsal and ventral face.

Rhexia mariana L.

All the specimens examined proved to be root-shoots. Some of them were quite young and vegetative, but I was unable to detect seedlings.[6] This species differs markedly from *R. virginica* in possessing no tuberous roots. The roots that produce the shoots are horizontal, very long and slender, and several shoots, both vegetative and floral, may be observed upon the same root; the lateral branches are thinner, lighter brown in color, and branch freely. The shoots in

[6] The seedling is described and figured by LUBBOCK in his work on seedlings (1:545), but no mention is made of the further growth or as to the occurrence of root-shoots.

this species are able to persist more than one season, since the buds borne on the basal nodes remain active and produce new shoots in the next year. But, as stated above, young as well as old shoots may be observed among each other on the same root, and consequently on its upper face. Two to four slender secondary roots develop from the basal internodes of the older shoots. No specimen was found in which there was any indication of the primary root, and it would be very interesting to know whether the seedling of this species behaves in the same way as that of *R. virginica*.

THE INTERNAL STRUCTURE OF THE VEGETATIVE ORGANS

The roots

It is only in the very thin lateral roots that the primitive structure may be observed. The epidermis shows but little tendency to produce hairs; the exodermis consists of a single layer of thin-walled, pentagonal cells that are larger than those of the adjoining cortex. The cortex is of five layers of thin-walled cells, with wide, rhombic, intercellular spaces; druids but no deposits of starch were observed. A thin-walled endodermis and a continuous pericambium surround five groups of leptome, alternating with five short rays of hadrome; while the center of the stele is occupied by a narrow cylinder of moderately thickened conjunctive tissue.

In the thicker and stronger roots, lateral or secondary, the cortex frequently collapses radially, and there is increase in thickness; however they do not increase as much as do the roots of the foregoing species, and never become tuberous. Cork is developed when the secondary leptome and hadrome begin to appear, arising from the pericambium.

As stated above, the roots of this species are very long and grow horizontally and in several cases an excentric growth was noted. In old roots the epidermis and exodermis are partly thrown off, and the cortex is collapsed almost throughout. The stele, however, is protected by four or more strata of cork, within which there are stereids scattered in small groups outside the leptome; the secondary rays of hadrome are relatively short and separated from each other by mostly three rows of thick-walled parenchyma, which also occurs in the central part of the stele. No starch was observed.

The stem

The basal internodes are cylindric; those above are obtusely quadrangular, with four very narrow wings; hairs like those described under the foregoing species cover the stem. The cuticle is very prominently wrinkled, and the epidermis is thin-walled. The cortex is broken down in wide lacunes in the basal internode, but solid in the upper internodes. No collenchyma or stereome was found in the stem. There is only one small collateral mestome strand in each of the four wings, and sometimes one or two between them. The stele represents two arches within the slightly convex faces of the stem, and consists of bicollateral mestome strands with much leptome on the inner face of the hadrome. The pith is thin-walled and does not contain any isolated central strand of leptome; neither druids nor starch were observed. Pericyclic cork is developed, but only in the basal internodes.

The leaf

The cuticular striations over the ventral epidermis (*figs. 8* and *16*), which radiate toward the center of the outer cell wall, are characteristic of the leaf structure. The lumen of the epidermis is considerably wider on the ventral surface than on the dorsal, and the stomata (*fig. 7*) are not confined to the latter. They show the same structure as those of the other species, and some were noticed on the ventral face of the leaf-blade. Hairs of both kinds described above are scattered over both faces, and also along the margins. The chlorenchyma shows the same structure as observed in *R. virginica*, but the pneumatic tissue is less open. The midrib lacks the supernumerary ventral mestome strand, but otherwise the structure of the veins is identical with that of the former species.

Summary

Considered from an anatomical point of view, these two species may be distinguished from each other by the following contrasting characters:

R. virginica.—Roots tuberous where the shoots develop; no stereids outside the leptome of the root; stem broadly four-winged, with three mestome strands in each wing; one central mestome strand in the pith; no cuticular striations above ventral epidermis of leaf;

stomata only on dorsal face; midrib with a supernumerary mestome strand; clavate glandular hairs on dorsal face of leaf.

R. mariana.—Roots slender throughout; stereids outside the leptome of the root; stem narrowly four-winged, with one mestome strand in each wing; no central mestome strand in the pith; cuticular striations very distinct above ventral epidermis of leaf; stomata on both faces of leaf; midrib without a supernumerary mestome strand; clavate glandular hairs on both faces of leaf.

Common to both species are the bicollateral mestome bundles of stem and leaf; the absence of specialized subsidiary cells around the stomata; the absence of mechanical tissues (stereome and collenchyma); the occurrence of two types of glandular hairs; the bifacial structure of the leaves; and the ability of the roots to produce shoots.

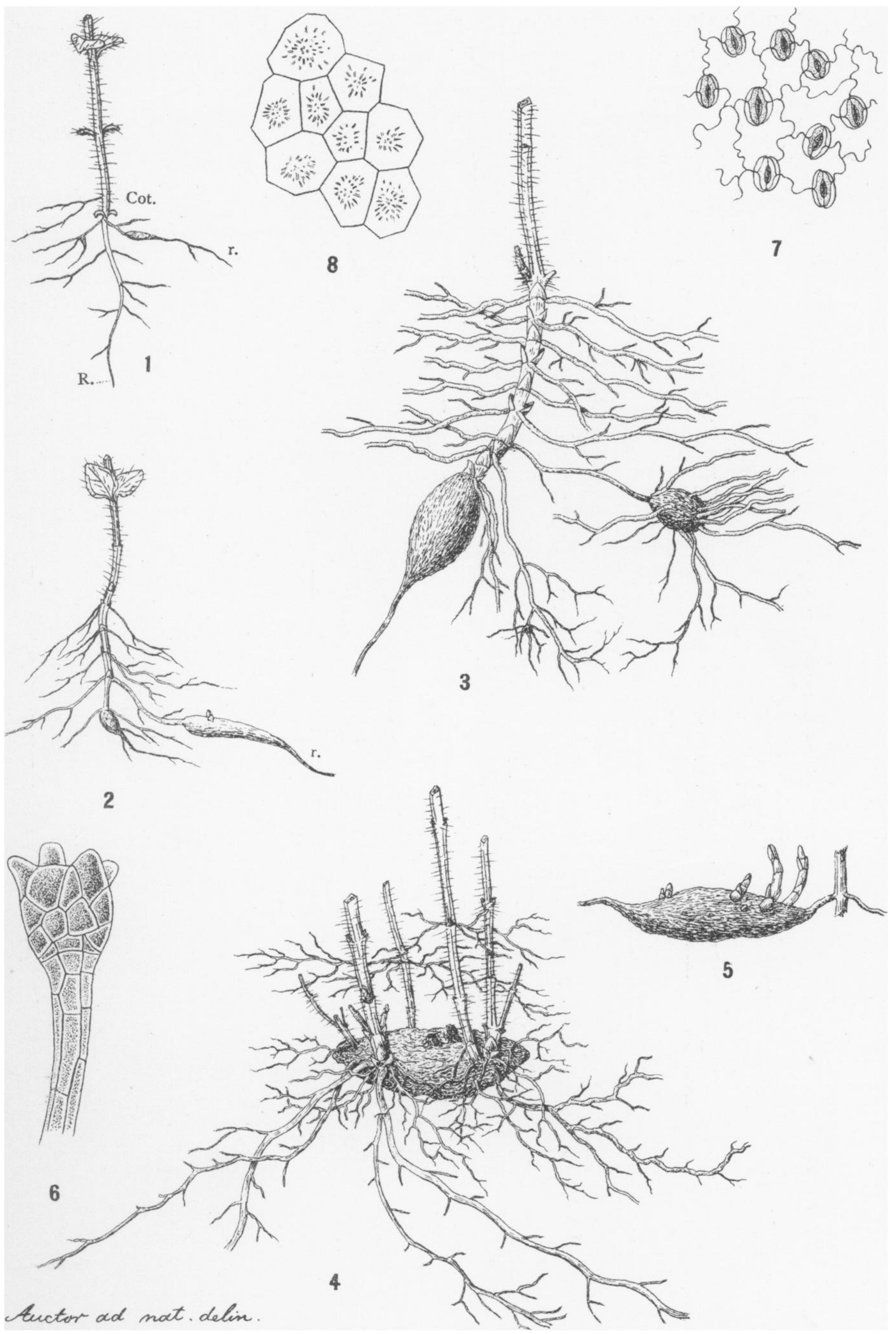
Vegetative propagation, therefore, depends upon the development of root-shoots, and, upon examining herbarium material, the same mode of propagation was found in *R. lutea* Walt., in which the roots are very long and slender, and the base of the shoot may persist for more than one season, *R. lanceolata* Walt., *R. serrulata* Nutt., and *R. ciliosa* Michx. All agree with *R. mariana* in the roots being slender and able to produce shoots. In *R. serrulata* one specimen appeared as if it was a seedling and blooming in the first season; and one specimen of *R. floridana* Nash had a tuberous root in addition to the slender, shoot-bearing root.

I believe that Rhexia must be placed with that type of plants in which the production of root-shoots is necessary to the normal development of the individual. It is a type poor in representatives, and WITTROCK enumerates species of Cirsium, Linaria, Convolvulus, Thesium, Coronilla, Epilobium, and Euphorbia as representing it. *Thladiantha dubia* Bge. doubtless belongs to this same category, according to SACHS,[7] who states that "the yearly regeneration is dependent upon root-shoots which develop from tuberous swellings of the very long and slender roots." The internal structure of the roots of this curcurbitaceous plant is described by SCOTT and BREBNER,[8] but is very different from that observed in Rhexia.

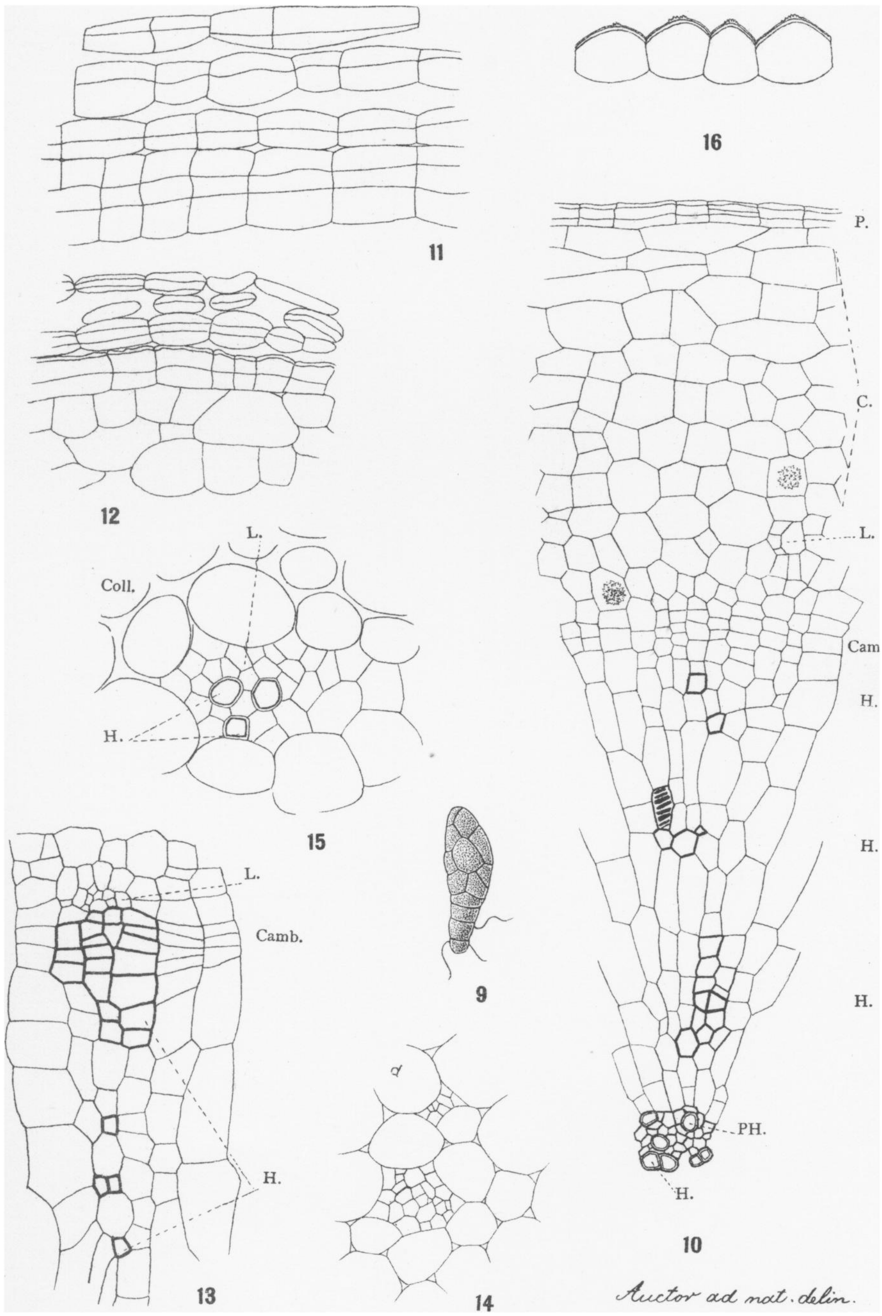
BROOKLAND, D. C.

[7] Vorlesungen über Pflanzen-Physiologie 28. Leipzig. 1882.

[8] Annals of Botany 5:273. 1890.



HOLM on RHEXIA



HOLM on RHEXIA

EXPLANATION OF PLATES I AND II

PLATE I

Rhexia virginica

FIG. 1. Seedling, showing basal internodes, cotyledons (*Cot*), primary root (*R*), and a lateral root with the tuberous swelling (*r*). $\times 1\frac{2}{3}$.

FIG. 2. A root-shoot developed from tuberous root of seedling; a lateral root swollen (*r*) and showing bud which will develop a shoot during next season. Natural size.

FIG. 3. The underground portions of a mature root-shoot; one of the secondary roots bears a tuber. Natural size.

FIG. 4. An old tuber with shoots. Natural size.

FIG. 5. An old tuber with buds. Natural size.

FIG. 6. Apex of a long glandular hair. $\times 320$.

PLATE II

Rhexia mariana

Fig. 7. Epidermis of lower face of leaf. $\times 320$.

FIG. 8. Epidermis of upper face of leaf. $\times 320$.

Rhexia virginica

FIG. 9. Glandular hair. $\times 320$.

FIG. 10. Transverse section of the tuberous root of *fig. 2*, showing cork (*P*), secondary cortex (*C*) with druids, leptome (*L*), cambium (*Cam*), hadrome (*H*), and protohadrome (*PH*). $\times 204$.

FIG. 11. Cork of the same tuber. $\times 320$.

FIG. 12. Cork of an older tuber. $\times 320$.

FIG. 13. Transverse section of an old tuber, showing outermost part of a mestome strand; index letters as above. $\times 320$.

FIG. 14. Central leptome strand of stem. $\times 320$.

FIG. 15. Ventral supernumerary vein of leaf, also showing thick-walled colorless tissue (*Coll*), leptome (*L*), and hadrome (*H*). $\times 560$.

FIG. 16. Transverse *Rhexia mariana* section of ventral epidermis of leaf. $\times 320$.